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A contribution to the embryology of *Erigeron karwinskianus* var. *mucronatus*

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Erigeron karwinskianus var. *mucronatus* の胚学的研究

Embryological studies in the tribe Astereae are quite extensive and these have been reviewed by Harling (1951) and Pullaiah (1978, 1984). A perusal of the literature reveals that the embryology of *Erigeron karwinskianus* DC. var. *mucronatus* DC. was studied earlier by Carano (1921), Fagerlind (1974) and Battaglia (1950). However, their studies are confined to the female gametophyte development only. Hence, the present study was undertaken to know the complete life history of *Erigeron karwinskianus* var. *mucronatus*.

Material and methods The material was collected by Dr. T. Pullaiah from Nilgiris in Tamil Nadu. Flowers heads of various sizes were fixed in formalin-acetic-alcohol (F. A. A.). Usual methods of dehydration, embedding and sectioning were followed. The sections cut at a thickness of 4–8 μm were stained in Delafield's haematoxylin. Voucher specimen no. 3097 was deposited in the Herbarium of Sri Krishnadevaraya University.

Observations Microsporangium, microsporogenesis and male gametophyte. The anthers are four-lobed (Fig. 1F). In each lobe, 4 or 5 archesporial cells get diffetentiated hypodermally (Fig. 1A). These cells by undergoing periclinal division produce primary parietal layer towards epidermis and primary sporogenous cells towards inside (Fig. 1B). The primary parietal layer again undergoes another periclinal division giving rise to an inner tapetum and outer parietal layer (Fig. 1C). The latter again divides periclinally forming hypodermal layer below the epidermis and a middle layer above the tapetum (Fig. 1D, E, G) thus resulting in Dicotyledonous type of anther wall development (Davis 1966).

The epidermal cells undergo only anticlinical divisions to cope up with the expanding anther. The hypodermal layer develops fibrous thicknings at the

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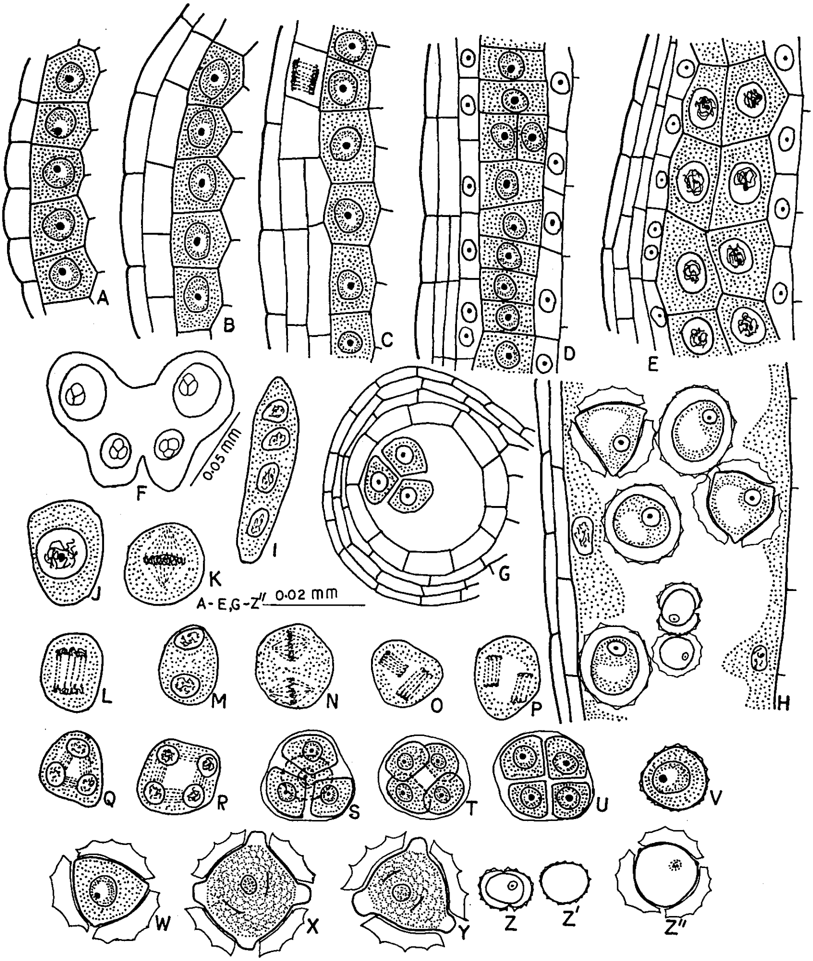

Fig. 1. *Erigeron karwinskianus* var. *mucronatus*. A–E. Longitudinal sections of parts of anther lobes showing development of wall layers. F. Transverse section of part of tetrasporangiate anther. G. Transverse section of part of anther lobe enlarged from Fig. F. H. Longitudinal section of part of anther lobe showing periplasmodial tapetum. I. Anther tapetal cells. J–R. Pollen mother cells in meiotic division. S–U. Tetrahedral, decussate and isobilateral microspore tetrads respectively. V–W. Uni-nucleate pollen grains. X–Y. Mature pollen grains. Z–Z″. Sterile pollen grains.

time of formation of mature pollen grains and the middle layer is ephemeral. Tapetal cells undergo nuclear divisions and fusions resulting in multinucleate and polyploid anther tapetal cells (Fig. 1I).

The tapetum is of the amoeboid type. At about the time of formation of one-nucleate pollen grains, the walls of the tapetum break down and the cytoplasm (Fig. 1H) finally coalesces in the centre forming periplasmodium. The tapetum is completely absorbed by the developing pollen grains.

The primary sporogeneous cells undergo transverse and vertical divisions forming two rows of pollen mother cells (Fig. 1E). The pollen mother cells round off and undergo meiosis followed by simultaneous cytokinesis (Fig. 1J–R) resulting in tetrahedral, decussate and isobilateral microspore tetrads (Fig. 1S–U). The microspores after separation from the tetrad, enlarge and develop thick exine (Fig. 1V, W). Pollen grains at the time of anthesis are 3-celled with three germ pores (Fig. 1Y). Pollen grains with four germ pores are also met with (Fig. 1X). Two types of micro sterile pollen grains also occur. One of them is with a small nucleus while the other is without any contents (Fig. 1Z, Z′). Though the former increases in size, its nucleus degenerates (Fig. 1Z″) and thus both types of pollen grains become sterile. These sterile pollen grains constitute about 15% of the total pollen grains.

Ovary and ovule. The ovary is inferior, bicarpellary, syncarpous and unilocular with a single basal anatropous, unitegmic and tenuinucellate ovule (Fig. 2A, B). During megaspore tetrad formation, the inner epidermis of the integument becomes differentiated as integumentary tapetum (Fig. 3B). This layer remains uniseriate with uninucleate cells throughout its further growth.

Megasporogenesis and female gametophyte. The female archesporial cell is hypodermal and it directly functions as a megaspore mother cell (Fig. 2A). The female gametophyte may develop either in apomictic manner or in normal sexual manner according to *Drusa* type.

When the embryo sac develops in normal sexual manner, the megaspore mother cell undergoes the usual meiotic divisions not accompanied by wall formation either at meiosis I or at meiosis II resulting in a coenomegaspore of four nuclei (Fig. 3A, B). The arrangements of the nuclei in a coenomegaspore may be either 1+2+1 or 1+3 manner (Fig. 3C, D). They undergo two mitotic divisions, but one or two chalazal nuclei fail to undergo divisions resulting in thirteen or ten nuclei. They organise into three-celled egg apparatus, two nuclei fuse to form secondary nucleus while the rest of the nuclei are cut off as antipodal cells (Fig. 3E). This type of development according to Maheshwari (1950) is of the tetrasporic *Drusa* type. The synergids are hooked. The antipodal cells may range from 3-7 (Fig. 3E-H) and are persistant up to the globular stage of the embryo (Fig. 4A-C).

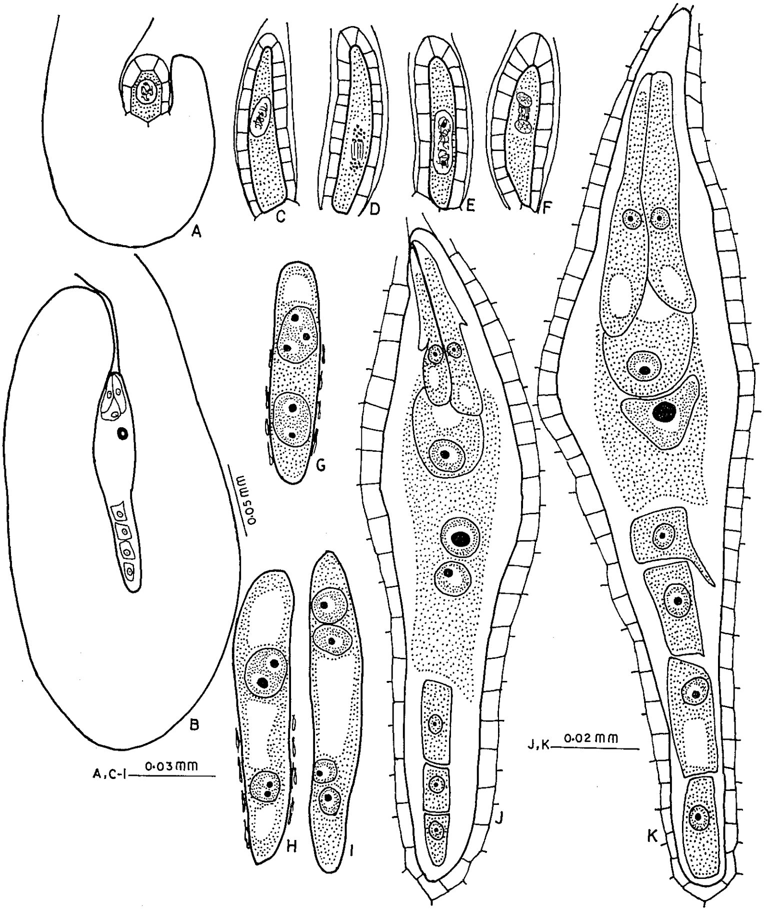

Fig. 2. *Erigeron karwinskianus* var. *mucronatus*. A. Ovules at megaspore mother cell and embryo sac stages respectively. C-D. Megaspore mother cell in meiosis I. E. Restitution nucleus. F. Meiosis II. G, H. 2-nucleate embryo sacs. I. 4-nucleate embryo sac. J, K. Young and mature embryo sacs respectively.

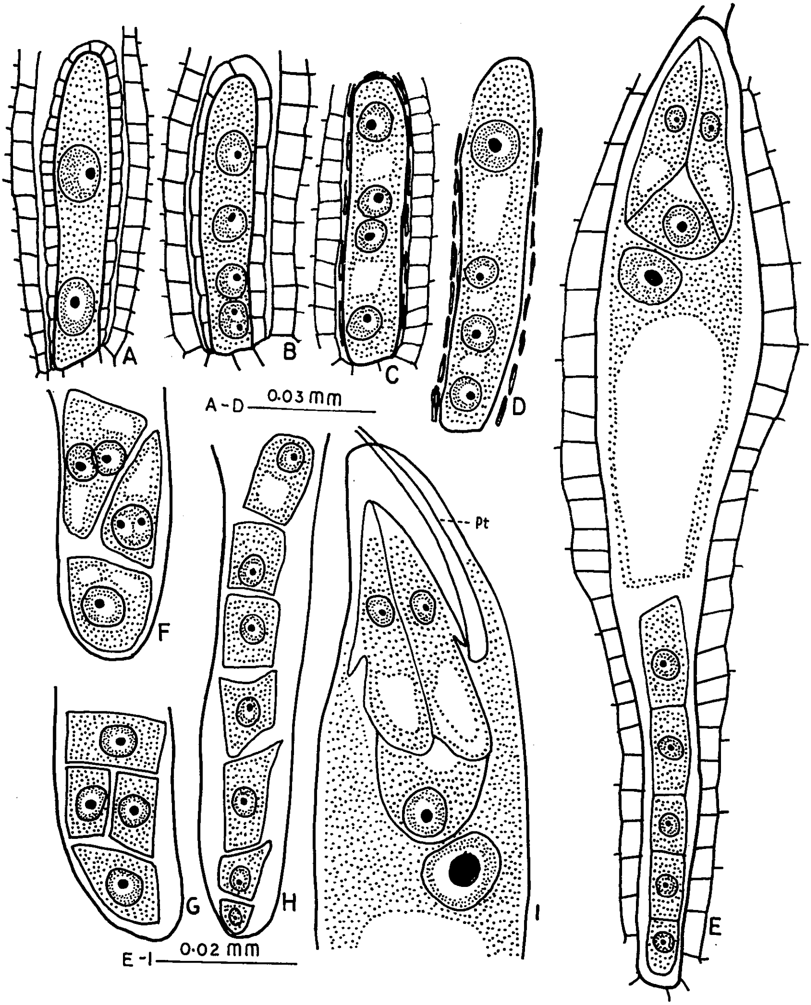

Fig. 3. *Erigeron karwinskianus* var. *mucronatus*. A. 2-nucleate gynospore. B-D. Coenomegaspores. E. Mature embryo sac. F-H. Antipodal cells. I. Micropylar part of the embryo sac showing pollen tube, egg apparatus and secondary nucleus (pt: pollen tube).

Apomixis. In 50% of the ovules, the development of embryo sacs follow *Ixeris* type of aneuspory. Here, the megaspore mother cell undergoes meiotic division in which meiosis I (heterotypic) is irregular and meiosis II (homotypic) is normal. During heterotypic division of the megaspore mother cell, pairing and formation of two separate groups of chromosomes is omitted. At anaphase, the chromosomes become enclosed in a common nuclear membrane forming a restitution nucleus (Fig. 2C-E). Thus heterotypic division ends with a restitution nucleus. In homotypic division due to the suppression of cytokinesis, a binucleate gynospore results (Fig. 2F-H). The two nuclei later on take part in mitotic division resulting in an 8-nucleate embryo sac (Fig. 2J). The organisation of the egg apparatus, polar nuclei and antipodals is essentially similar to its normal sexual embryo sac but the egg apparatus is comparatively larger (Fig. 2K). The synergids are hooked and are persistent (Fig. 4D, E). The two polar nuclei fuse to form secondary nucleus which lies near the egg apparatus. The number of antipodals may increase from 3 to 4 only. This type of apomixis according to Battaglia (1963) is known as *Ixeris* type of aneuspory.

Fertilization, endosperm and embryo. The embryo sacs which develop in normal sexual manner show fertilization and endosperm development (Fig. 3I), whereas in the embryo sacs which develop in aneusporic manner fertilization is absent, the endosperm develops autonomously and embryo develops parthenogenetically (Fig. 4D, E). The entry of the pollen tube into the embryo sac is porogamous.

Endosperm development is of the cellular type. The primary endosperm nucleus divides mitotically followed by wall formation resulting in four cells. Further divisions in these cells take place in all directions and a massive tissus is formed filling the entire embryo sac with cellular tissue (Fig. 4A-C). Endosperm is consumed completely by the developing embryo except for one or two layers.

After undergoing a short period of rest, the zygote (or egg in aposporic embryo sac) divides transversely resulting in a proembryo of two cells *ca* and *cb*, the terminal and the basal cells respectively. The cell *cb* divides earlier than the cell *ca* resulting in a proembryo of three cells *ca*, *m* & *ci* (Fig. 5B). Later, the cell *ca* undergoes vertical divisions at right angles to one another resulting in the formation of quadrants *q* (Fig. 5C). The cell *m* divides vertically twice the walls being oriented at right angles to one another resulting in

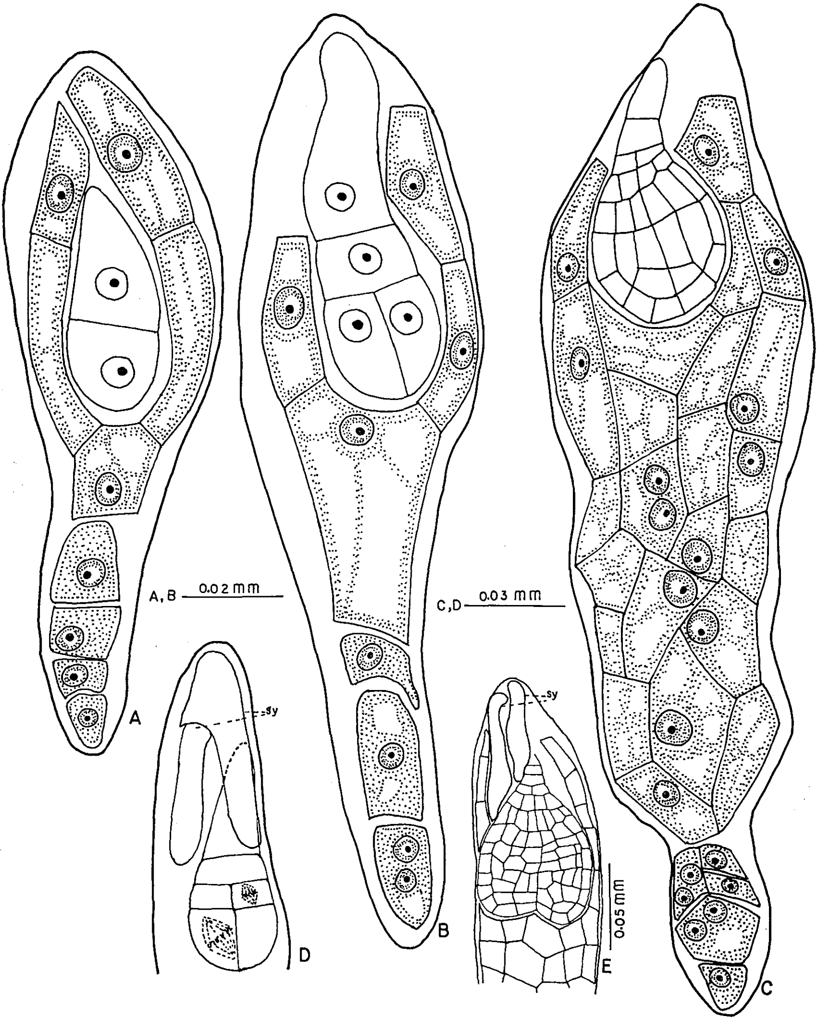

Fig. 4. *Erigeron karwinskianus* var. *mucronatus*. A–C. Stages in the development of endosperm. D, E. Micropylar part of the embryo sacs showing parthenogenetic embryos. Note persistant asynergids (sy : synergids).

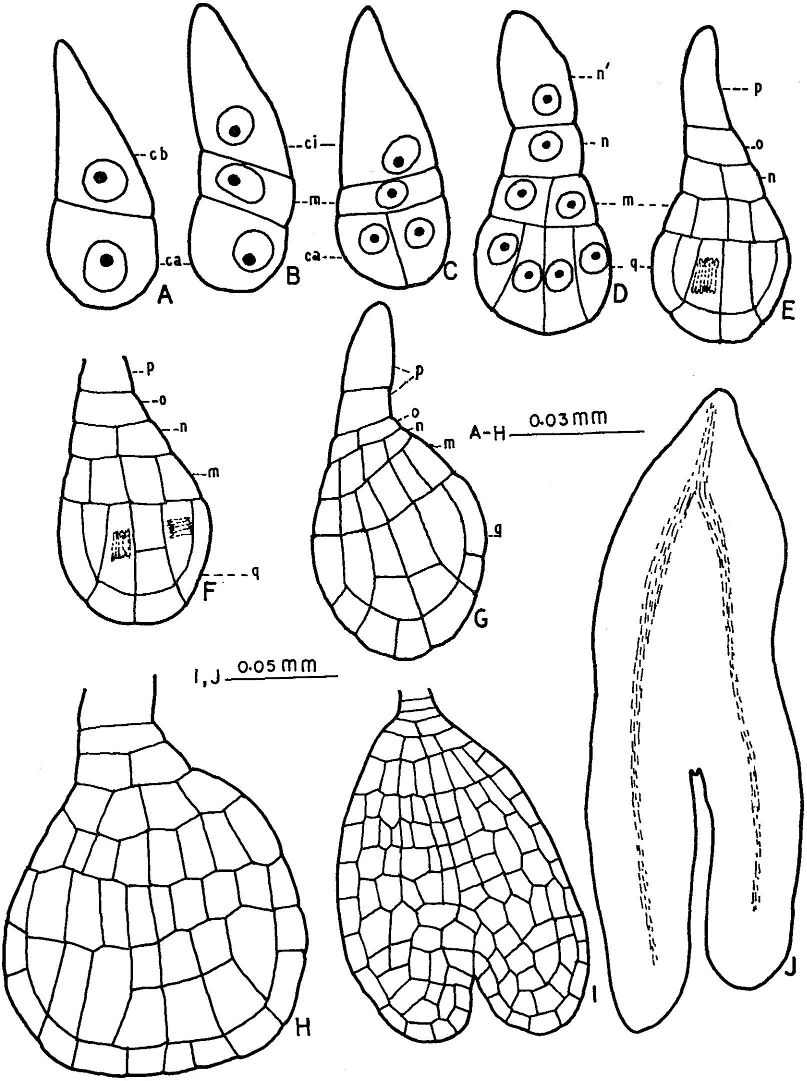

Fig. 5. *Erigeron karwinskianus* var. *mucronatus*. A-E. Various stages in the development of embryo.

quadrants (Fig. 5D). The cell *ci* divides transversely giving rise to two superposed cells *n* and *n′* (Fig. 5D). The tier *q* undergoes diagonal divisions resulting in octants. The cell *n′* undergoes transverse division forming *o* and *p* (Fig. 5E). The tier *q* gives rise to cotyledons and stem tip, *m* contributes to the hypocotyledonary region and plerome initials of root and *n* and *o* to the initials of root cortex, root cap and dermatogen. The cell *p* undergoes transverse division resulting in short suspensor. The embryo development thus follows the *Senecio* variation of Asterad type of Johansen (1950) and Grand period I, Megarchetype II, series A, sub series A_2 in the first embryonic group according th Souèges system (Crété 1963).

Discussion The tapetum is of the amoeboid type in all the investigated species of Asteraceae including the present study. However, Snow (1945) and Anderson (1970) reported glandular tapetum in *Chrysothamnus*. Since the presence of periplasmodial tapetum is characteristic of the family Asteraceae (Pullaiah 1984), the observations of Snow (op. cit.) and Anderson (op. cit.) seem to be erroneous.

The female archesporium is single-celled in *Erigeron karwinskianus* var. *mucronatus* as reported earlier by Carano (1921). More than one type of embryo sac development is reported in different species of the genus *Erigeron* (Harling 1951). Monosporic type occurs in *E. bonariensis* and *E. canadensis*, bisporic in *E. coulteri*, *E. elatior*, *E. macranthus* and *E. unalaschkensis* and tetrasporic in *E. annuus*, *E. aureus*, and *E. divergens* etc. In some species like *E. elatior*, *E. pulchellus* and *E. simplex* the female gametophyte development follows all the three, mono-, bi-, and tetrasporic types. Thus the genus *Erigeron* shows great diversity in the embryo sac development. Carano (1921) reported a tetrasportic type of female gametophyte development in *Erigeron karwinskianus* var. *mucronatus*. The present study in the above taxon reveals that embryo sac development follows *Drusa* type.

Erigeron karwinskianus var. *mucronatus* also shows apomictic type of embryo sac development. Carano (1921), Fagerlind (1947) and Battaglia (1950) reported *Taraxacum*, *Ixeris* and *Rudbeckia* types of aneuspory. In the present investigation the embryo sac development is in agreement with the above authors as far as the *Ixeris* type of anuespory is concerned. Other types of development are not met with.

The increase in the number of antipodals is noted in the present study which is in agreement with Carano (1921). Persistance of antipodal cells up to the globular embryo stage is observed in *Erigeron bonariensis* (Sharma & Murthy 1978) and *E. canadensis* (Rangaswamy & Pullaiah 1984).

The tribe shows both nuclear and cellular types of endosperm development. The type of endosperm development varies in different species of *Erigeron*. The embryo development in *E. karwinskianus* var. *mucronatus* (present study) follows the *Senecio* variation of Asterad type as in other members of the family Asteraceae

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Erigeron karwinskianus var. *mucronatus* の胚学的研究を行った。花粉のタペタム形成はアメボイド型である。胚囊形成には2通りあって，ひとつは *Drusa* type で，胚囊母細胞は4回核分裂して16核になるが細胞膜はできず，これが直接胚囊となる。16核の内から1個の卵細胞，2個の助細胞，2個の極核ができ，残りは1-2核をもつ2-7個の反足細胞となる。もうひとつは *Ixeris* type で，胞子母細胞が減数分裂せずに直接胚囊母細胞になり，3回分裂して8核となり，普通の胚囊を作る。この場合反足細胞は3個であるが，分裂して4個になることもある。*Drusa* type は授精によって胚と胚乳形成が行われるが，*Ixeris* type は授精せずに胚と胚乳形成が行われる。胚乳形成は細胞型である。胚形成はコンギク型サワギク変型である。

○ウメバチソウの紅葯品種

(大場秀章・梅津幸雄) Hideaki OHBA & Yukio UMEZU: A form with red anthers of *Parnassia palustris* L.

ウメバチソウ属は通常白または淡黄色の花を開く。また，葯の色はウメバチソウでは淡黄色（象牙色）である。ところが，最近大分県下で葯が紅色で，時に花弁も紅色を帯びたウメバチソウが見いだされた。ウメバチソウ属でこのような変異が他にも知られているかどうか明らかにできなかったが，少なくともウメバチソウでは未知のようである。

生育地は，山間の水田ののり面である。のり面の上部はスギ林に覆われているが，その最下部は草刈りにより維持されていると考えられる草地で，そこにウメバチソウが生育している。紅葯の個体は他にも数個体あった。普通の白花・淡黄色葯のウメバチソウは，のり面に多数見られた。

材料を提供され研究の機会を与えて下さった大分県在住の麻川尚良氏にお礼申し上げます。

Parnassia palustris L. var. *multiseta* Ledeb. f. **rhodanthera** H. Ohba et Umezu, f. nov.

A typo antheris ante dehiscentam carmineis etiam saepe petalis dilutissime incarnatis bene differt.

Nomina jap. Beni-shibe-umebatisô, nov.

Typus. Japonia. Kyushu: praef. Oita, Orito oppidi Yabakei, alt. 260 m (Takao Ono et Takayoshi Asakawa, 18 Oct. 1984, TI)

（東京大学 総合研究資料館植物部門・福岡県築上郡吉富町幸子）